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PHOTOPERIODICITY IN BIRDS[1]

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> In the spring a fuller crimson comes upon the robin's breast;
> In the spring the wanton lapwing gets himself another crest;
> In the spring a livelier iris changes on the burnished dove;
> In the spring a young man's fancy lightly turns to thoughts of love.
> —*Tennyson, Locksley Hall.*

INTRODUCTION

It has long been recognized that various activities of birds are related to the daily cycle of light and darkness and to seasonal change from short days in winter to long ones in summer. In one case notice has been taken of an apparent relation to time at which increasing moonlight from waxing moons in spring adds its stimulus to that of lengthening days. These photoperiodic activities are various and include daily times of waking and beginning of song and bodily activity, daily changes in the periods of sporulation of bird malarias and other typical cyclic diseases, seasonal changes of plumage, migrations, periods of sexual activity and quiescence accompanied by changes in breeding behavior and courtship display.

It is proposed to discuss, rather incompletely, but as suggestively as possible in small space, selected phases of this apparent dependence of the activities and functions of birds upon variations in daily and seasonal illumination as factors in their environment. It is emphasized from the first that many other factors in their environment also affect the physiology and behavior of birds, often more profoundly than do changes in exposure to light. There also appear to be intrinsic rhythms more or less independent of environmental influence. This paper will merely bring out relations to the light factor without excluding others.

Martin said, in "A Voyage to St. Kilda" (London, 1698), "The inhabitants observed that when the April moon goes far in May the fowls (sea birds) are ten to twelve days later in laying their eggs than ordinarily they use to be." This implies a summation effect of length-

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ening days and waxing moonlight upon the incidence of reproduction in sea birds. Sharpey-Schafer (1907), on theoretical grounds, suggested that duration of daylight "may well be considered a determining factor in migration, and it has the advantage over other suggested factors that it applies to the northerly as well as to the southerly movement." But he considered it improbable that migration is the result of developmental changes in the sexual organs, since the sex-glands of spring migrants are still almost as small as in autumn. Such early suggestions regarding physiological and behavioristic photoperiodicity of various types as exhibited by birds may be multiplied almost *ad lib.*

Daily Rhythms

Temperature

Kendeigh (1934) has discussed daily rhythms of birds very thoroughly. He points out a daily rhythm of body temperature and metabolism, highest at noon or early afternoon in sparrows and lowest near 2:15 A. M., in part related to exercise, but rising before the birds leave the nest in the morning. Under starvation, very low temperatures, etc., survival time is shortest and loss of weight greatest in the light and longest in darkness or in winter time when periods of light are shortest (63 per cent greater than in summer). Summer birds survive high temperatures better than winter ones, though loss of weight before death is not consistently different. Winter birds have lower metabolic rates, temperature for temperature, than summer birds and greater average weight. Wrens differ from sparrows only relatively in these respects. Average night temperature and number of hours of darkness without food are important factors in survival time under starvation, both related to length of day. Other authors do not emphasize the temperature factor so much but stress duration of daylight and feeding periods. Kendeigh points to daily maximum temperature as the critical factor. Continuous light reduces survival time, at high temperatures. Temperature x hours of darkness constitute the critical factor for survival at low temperature.

Daily Activities of Day and Night, or Twilight, Foragers

There can be little doubt that times of roosting, of evensong, and of return from foraging are controlled by the decreasing of light-intensity and the coming of twilight in birds that hunt by day. With such birds the time of morning song, of leaving the nest or roost, and even cock-crow are related to incidence of daylight and vary in correlation with it (Allard, 1930; Shaver and Walker, 1931; Lutz, 1931; Wynne-Edwards, 1930).

On the contrary, in birds, like flycatchers of some species, night hawks, owls, etc., that hunt by twilight or night, there is increased activity when light-intensity recedes to varying degrees. In caged birds that are migratory there is increased activity at night during the seasons of spring and fall migration for the species (Wagner, 1930).

Mitotic Rhythms in Sex-glands

Foley (1929) and Riley (1936) found a diurnal rhythm of spermatogenesis in sparrows, with active mitoses confined to the period of darkness. Reversal of light and dark periods leads to a change over of these mitoses from between 2:00 and 4:00 A. M. to the afternoon hours. The wave of mitotic activity is dependent upon lowered body temperature. If body temperature is lowered experimentally during the light hours, mitotic figures appear within two hours; if birds are kept active during night hours and temperature thereby kept up, spermatogenesis is retarded. Injections of gonadotropic hormone cause rapid increase in the size of gonads, attributable largely to increased activity at low body temperature at night. Riley reasons that the spermatogenic cycle is controlled by a combination of environmental and internal factors; that reduction of body temperature in the dark period makes the germ-cells responsive to stimulation by the gonadotropic hypophysial hormone.

Avian Blood Diseases

Boughton (1932, 1933) and Boughton, Atchley, and Eskridge (1935) pointed out a diurnal rhythm in avian isospora with diurnal oöcyst production in the sparrow modifiable experimentally by changes in the length of the periods of light and darkness to which host birds are exposed. They conclude that peaks of oöcysts can not be explained as due to ingestion of infective material nor to increased fecal discharge during the feeding periods, which Boyd (1929, 1933) considered to be important in controlling reproductive periods in *Plasmodium cathemerium*, the parasite in canary malaria. They found that the mechanism controlling the periodic production of oöcysts operates in a light-dark period which precedes the appearance of oöcysts by approximately forty-eight hours. Daily activity of the host appears to be the primary factor. Otherwise the reproductive cycle appears to resemble the periodic asexual sporulation of the plasmodium of the canary, in which Boyd (1933) found no relation to fatigue of the host. Wolfson (1936a, 1936b, 1937) also found a relation of plasmodium species (3) to daily light cycle.

Manwell and Herman (1935) find at least seven species of malaria in birds and several others that are as yet questionable. Incidence is higher in migratory birds and in those going farther south than in non-migrants. Ducks and swallows are infected with a malaria-like disease due to *Leucocytozoön anatis.* The infection occurs principally when the birds roost near streams where the black fly vector of the disease breeds. So, much is to be done in study of the relations of these diseases to environmental factors.

Some of these diurnal rhythms of birds and of some of their blood parasites correlated with internal physiological rhythms of the birds are directly conditioned or controlled by the light-dark cycle, while others are only indirectly so through consequent cycles of temperature, physical activity and fatigue, and maximum and minimum consumption of food. Some may therefore be described as primarily photoperiodic; others as only secondarily so. In most cases the complete and exact mechanism involved is still only partly known or open to controversy. Much further study of these phases of physiological activity and behavior is required and this is a most fertile field for ornithological study.

SEASONAL RHYTHMS

Temperature, Basal Metabolism, Thyroid Activity

Since Kendeigh (1934) has discussed these phases thoroughly it is enough here to draw attention to some of the findings bearing on these cycles. Riddle and Fisher (1925) and Haecker (1926) found that thyroid activity is greater in winter cold than in warm summer months. This affects basal metabolism. But Kendeigh (1934) found that winter birds withstand low temperatures better than summer ones, and summer ones high temperatures the better; that winter birds have lower basal metabolic rates, temperature for temperature, higher initial body weights and a lower rate of loss of weight than summer birds, under starvation. Plumage weight is greater for adult birds in winter than in summer. Even in summer it is greater in adult than in juvenile birds. Beebe (1908) and Walton and Marshall (unpublished data) found that plumage changes in some birds (Scarlet Tanagers, Bobolinks, wild ducks) are conditioned by light cycles.

Kendeigh found that the average night temperature plus the number of hours of darkness without food are the important factors in determining survival time of birds under starvation. Groebbels (1927-1932) emphasizes duration of daylight rather than darkness and stresses temperature much less as a factor. Rowan (1931) emphasizes shortness of feeding time per day in winter and short days as a limiting factor which prevents the gathering of enough food by some species. Survival time is shortened by high humidity at high temperatures, by continuous light, increased activity and winds. Species of birds is a factor in all cases. The above factors are related to length of day and intensity of light.

Seasonal Abundance

Shaver (1933) found that the factors related to seasonal abundance of birds in order of importance are temperature, duration of sunshine, relative humidity, wind velocity, atmospheric pressure, and precipitation. This is related to movements of migratory species and, as will be shown below, is related to seasonal and even to daily cycles of light and dark periods. Consumption of food is greater per day in summer than in winter (Groebbels, 1931; Rörig 1905) correlated with higher temperature, metabolism, and activity of many body tissues of which spermatogenesis and ovogenesis are but two.

Plumage

Differences in weight and thickness of plumage with the seasons have been mentioned above. Many birds also pass through one or more changes in type and coloration of plumage each year in correlation with the seasons. Molting occurs in many birds in late summer and early autumn when temperatures are high and the heavier coat is put on at this season (Kendeigh, 1934). For birds in the temperate zones this is just a short time after the change over from lengthening days of increasing light intensity to decreasing intensity and shortening days and the taking on of the heavier coat occurs when temperatures are still relatively high; therefore cold could hardly be a factor in causing the change.

Some species, like mallard ducks, tanagers, bobolinks, lapwings, or even pheasants and domestic fowl, take on a different plumage or assume brighter head furnishings before or at the breeding season, or in autumn and spring to assume less striking colorations at the season for incubation or rearing the young, in contrast to showy breeding plumage. Others like Starlings and sparrows, change the color of their bills under the influence of the hormones from the gonads or the hypophysis, with the seasons. Even the plumage changes have been shown to be dependent upon changed hormone action of the thyroid and pituitary, as well as the sex-glands, and these upon changes in daily period and intensity or wave-length of light (Beebe, 1908; Goodale, 1910; Seligman and Shattock, 1914; Bissonnette, 1930 *et seq.*; Keck, 1932, 1934; Witschi and Keck, 1935; Tallent, 1931; Jaap, 1934;

Miller, 1935; Zawadowsky, 1929; Walton and Marshall, unpublished data; Bissonnette and Csech, 1936b).

Sexual Photoperiodicity

It has long been known that sex-glands, secondary sexual apparatus, sexual behavior, and related activities, including changes of plumage and erectile head furnishings, in many birds are subject to seasonal changes. Tennyson, in "Locksley Hall", wrote the stanza at the head of this paper.

It was taken for granted till recently that these rhythms were conditioned and controlled directly by the succession of warm and cold seasons, through temperature.

Studies on this subject published before 1934 have been reviewed by Bissonnette (1935, 1936c) and Walton (1933) for animals in general, and by Kendeigh (1934) in connection with the influence of environmental factors upon the physiological rhythms of birds. The latter showed that nesting and laying are considerably modified and controlled by changes in temperature. Sudden drops in temperature interrupt nesting and laying and postpone incubation. But these are only secondary variations in the reproductive cycles of birds, superimposed upon a more fundamental primary drive to reproductive activity.

Rowan (1925-37) first showed that reversing the daylight curve in autumn and winter with electric lighting would cause the sex-glands of juncos, canaries, and crows to enlarge and produce sperms in winter instead of at the normal time in April or May. This was correlated with migration and will be discussed somewhat more fully under that topic because much of the work on migration can not be dissociated from that on sexual photoperiodicity. Duplication to some degree can not be avoided unless the two topics are reviewed together.

Weak light from electric bulbs, added after nightfall in increasing periods and then withheld periodically, brought about the breeding condition four or more times in a year. Rowan came to the conclusion, based upon an experiment with increased exercise instead of increased light with birds already well stimulated with light increases, that it was the increasing periods of exercise and wakefulness rather than increase of light, as such, that was the fundamental cause of the stimulation to increased sexual activity in juncos. This he still maintains though he uses light as his activating factor in his subsequent experiments and not exercise, and in the face of increasing evidence that, in all other animals tested and showing this reaction, it is light, *qua* light, that is the primary stimulus. Amount of food consumed did not appear as a factor in the reaction, at least when it was varied and sufficient to prevent inanition. The work of Bissonnette (1930 *et seq.*) and others supports the statement that amount of food consumed is of relative unimportance. But it is quite evident that inadequate variety of food or improper quality, so far as salts, vitamins, proteins, and fats are concerned, may act as a limiting factor preventing activation by the usual stimuli and may even play a more important rôle in some cases (Bissonnette, 1933b). Longer feeding periods or shorter night periods without feeding have been looked upon by poultry men as the cause of increased laying of fowl in autumn and winter when they are subjected to "night-lighting". But the experimental studies on birds by Rowan (1925-37), Cole (1933), Miyazaki (1934), Benoit (1934-6), Petty (Brill, 1934), Martin (1935), Riley (1936), Scott and Payne (1937), Keck (1932), Kirschbaum and Ringoen (1936), Bissonnette (1930-37), Bissonnette and Wadlund (1931-3), Bissonnette and Csech (1936a, b, c, 1937), Clark, Leonard, and Bump (1936, 1937) and others, and similar studies upon mammals and amphibia (Bissonnette, 1935, 1936c) rather indicate that the larger consumption of food is the result of increased reproductive activity, caused by increased lighting, instead of its cause.

Between 1926 and 1928, Bissonnette (1930a, b) and Bissonnette and Chapnick (1930), and since that time, Bissonnette and Zujko (1936) studied the normal sexual cycle of the European Starling (*Sturnus vulgaris*), a bird which at that time migrated but little in this country. Of all environmental variables studied in correlation with this cycle, the seasonal change in duration of daily daylight periods was the only one which was regular enough to account for the very precise regularity of the recurrence of the various phases of the sexual cycle (Bissonnette and Chapnick, 1930).

Experimental studies were then begun to test the effects of altering the daylength by added illumination, in autumn evenings after sundown, along with those of similar periods of forced exercise, which Rowan (1928 *et seq.*) maintains is the fundamental factor inducing activation of the sexual apparatus in the junco and in birds in general with similar sexual cycles. Experiments were carried on from December to April inclusive, and repeated with variations in subsequent years. Added exercise periods without added light were not effective to induce sexual activity in the Starling and even tended to reduce the size and activity of the testes. Light added for the same periods, on the contrary, was very potent to induce activation of the sex-glands, in males more consistently than in females (Bissonnette, 1931a).

By modifying the experimental method and the previous sexual conditions of the birds used, it was found that increasing exercise periods led to a lag in onset of changes in the testes induced by changes in daylength, whether these changes consisted of increase of exposure to light, inducing increased activity of the testes, or of reduced lighting, leading to decreased activity of these glands. That is, if birds already undergoing increase of activity of their sex-glands stimulated by added lighting were changed from increasing to decreasing periods of light, the testes of those placed at the same time on increased exercise periods continued to increase in size and activity for a considerable time thereafter before undergoing regression or slowed activity. Those not put on increased periods of exercise, but with similar reduction of lighting periods, very quickly went over into regression or slowed down their activity, just as did Rowan's juncos. But the reverse experiment was also performed and birds undergoing regression from reduction of their daily light periods were divided into two groups. For one group the daily lighting was increased but forced exercise was not given. For the other group both forced exercise and added lighting were begun at the same time for similar periods daily. In those with increased lighting alone, there was an early response by increasing size and activity of the gonads. In those with equal periods of both added light and forced exercise, regression continued for a considerable time before activation by added lighting became operative. They then responded with somewhat more accelerated activation so that they often overtook the birds of the first group finally. This was taken to indicate that, while increased exercise was not itself an activating factor, it modified the response to lighting, the major factor in these cases. Of course it is dangerous to reason by analogy from one species to another. But the great similarity of the results of the first group of these experiments to those of Rowan with juncos under almost identical conditions make them highly suggestive; though strictly speaking, as he says (Rowan, 1937), they may prove nothing. They do, however, make it impossible to accept his conclusions for birds in general and show that his are not the only valid conclusions from his data, even with juncos.

Further studies (Bissonnette, 1931b, 1932a; Bissonnette and Wadlund, 1931, '32, '33), aided by grants from the National Research Council, Committee for Research in Problems of Sex, showed that the rate or degree of stimulation of testis activity in a given time varies with the intensity of illumination used. Birds under a 10-watt bulb were slower to reach maximum activity than those under a 15-watt one at the same distance, and these again than those under a 25-watt bulb, and so on, with equal periods of exposure. Birds with added periods of both light and forced exercise were slower to begin activity, but later often overtook those with only added light of similar intensity and duration. The optimum intensity or duration of the daily period have not been determined as yet; but that such an optimum intensity at least exists is already evident.

The degree of stimulation for Starlings depends also on the color or wave-length of visible light used, not on its ultra-violet content (Bissonnette, 1932a; Bissonnette and Wadlund, 1931, '32, '33). Red is very highly stimulating; green of equal luminous intensity, used for the same daily periods, is not stimulating at all; white is less stimulating than red, probably because of smaller content of red or other stimulating rays. With much lower luminous intensity, violet was not stimulating but the testes appeared to decrease slightly in size as compared with those of controls receiving no added exposure to light. This difference in the effect of red, green, white, and violet lights was not due to difference in heat or total energy intensity, as measured by a thermocouple, but to apparent wave-length specificity. Benoit's (1934 *et seq.*) work with ducks has confirmed these findings in general and even as to most of the details. He finds that green and violet are not stimulating while reds and yellows are. Scott and Payne (1937) with turkeys, find red and white effective, but blue ineffective.

That this strictly localized wave-length specificity in the visible spectrum is not found in all animals was shown by Marshall and Bowden (1934, 1936). They found that for ferrets all wave-lengths tested from near infra-red through near ultra-violet were approximately equally effective. Animals subjected to near ultra-violet had greatly prolonged sexually active periods. Bissonnette (1937), however, found prolonged oestrus in ferrets brought into heat early in spring by experimental lighting with little or no ultra-violet. Beyond these limits Marshall and Bowden found no wave-lengths effective. They found that if time times intensity were constant, approximately constant degrees of activation resulted. So it is evident that, even among birds showing photoperiodicity, all wave-lengths will not be equally effective and the most effective ones will probably vary with different species if not with different strains of the same species.

Improper food, low in salts, proteins, vitamins, and fats, even if sufficient in quantity, acts as a limiting factor which may prevent even highly stimulating exposures to light from inducing sexual activity or greatly reduce their effectiveness (Bissonnette, 1933b).

No mating or egg-laying under these experimental conditions was observed even in Starlings brought to complete sexual maturity as judged by histological criteria. Such activities in these wild birds must be controlled by factors not permitted by the crowded conditions in these experiments and not by mere histological fitness for breeding (Bissonnette, 1933a, 1933b). Cole (1933), using Mourning Doves, was the first to secure mating and viable eggs in winter with a bird of limited breeding season. These doves, however, breed in captivity normally. Since Cole's experiments, several others have induced birds to breed out of their normal season with good fertility and hatchability. Birds used were the Bob-white (Brill, 1934; Bissonnette and Csech, 1936c), turkeys (Scott and Payne, 1937, cited in Bissonnette, 1936c), pheasants (Martin, 1935; Bissonnette and Csech, 1936a, 1936b, 1937; Clark, Leonard, and Bump, 1936, 1937), ducks (Benoit, 1934, 1935f), Ruffed Grouse (Clark, Leonard, and Bump, 1936, 1937), canaries (unpublished data from several sources), and doubtless many others. Guinea fowls fail to respond to increasing light given in this manner (Scott and Payne, 1937). These birds, like guinea pigs which also fail to respond to similar treatment, are natives of the tropics where the factor of changes in relative length of day and night is small and, probably, the animals did not evolve in such a way as to use this factor as a releasing stimulus to induce or accelerate sexual activity at a season most favorable for survival of the young (Young and his students, cited from Bissonnette, 1936c). Neither do all animals of the temperate zones (spermophile ground squirrel, Moore, etc., cited from Bissonnette, 1936c; and African weaver birds, Witschi, 1935, which retain their original African cycles in spite of removal to Iowa).

In male Starlings, a maximum effect and consistent results were obtained by giving large and immediate increases in daily periods of light rather than by gradually increasing periods, even in autumn when periods of daylight were decreasing. This was not so consistent with females. In ferrets this was reversed and males required gradually increasing periods throughout or they underwent regression of the germ-cells while interstitial cells and accessory sex-organs responded completely (Bissonnette, 1932b, *et seq.*). Success in inducing pheasants, bob-white, raccoons and ferrets, of both sexes, to become fertile and potent at the same time and to beget living young was attained by gradually increasing daily periods of light in autumn and winter (Bissonnette, 1936d; Bissonnette and Csech, 1936a, 1936b, 1936c, 1937).

Rowan also obtained his greatest success with juncos in this way. With male Starlings, filtered red light of 1.7 foot-candles luminous intensity, acting for six hours each night from the start, after nine and a half hours of daylight, gradually decreasing with the season, in a basement room, induced complete spermatogenesis in twenty-three days in December and January. Other combinations including red light did it in eighteen days (Bissonnette, 1931a, 1931b, 1932a, 1936e). Scott and Payne (1937), however, found that if the additional light is given during the daylight hours as increased intensity and not after nightfall, it had no stimulating effect on sexual activity in turkeys.

Normally testis regression in Starlings occurs before June 8 or 15; no birds killed on or after those dates had remained in complete spermatogenesis (Bissonnette, 1930b). But daily periods of daylight still increase slowly till June 21, both in duration and intensity. Prolonged experimental studies, even with most potent schedules of lighting, showed that birds invariably passed the climax of activity after a time and underwent regression. This was due to "throwing out of gear" or development of refractoriness at some part of the sexual mechanism. Maximum size and activity of testes could not be maintained beyond a certain period which varied inversely with the effectiveness of the stimulus used for activation and bore some relation to the length of the other phases of the induced sexual cycle. Animals brought quickly into maximum activity remained completely active for a shorter time than those more slowly activated (Bissonnette, 1936e). This also occurs with male and female ferrets. Long continued injections of gonadotropic anterior pituitary hormones and "pregnancy urine" show this same sort of failure to maintain activity of sex-glands and secondary sexual characters in rabbits, rats, and monkeys (Bissonnette, 1936c, for citations). This has led some to believe that reactions against foreign proteins are concerned. But in these refractory reactions in Starlings and ferrets with photic stimulation there can be no foreign protein to react against, because the animal's own glands produce the hormone against the effectiveness of which refractoriness occurs. Nothing foreign is introduced into the system and no natural hormonic balance is disturbed.

Rapid development of this refractoriness is probably at the bottom of recurrent short sexual cycles with or without ovulation intervening, and rapid recovery leads to repeated cycles in polyoestrous animals. Quick activation followed by quick regressive phases with prompt recovery of activity, or slower cycles, in different species will account for differences in length of oestrous cycles from the five-day cycle of the mouse to the longer ones of other animals like ferrets and rabbits. The relative length of these cycles may also be subject to environmental interference by various types of stimuli, and may be suppressed temporarily for varying periods by such agents. Some such factor operative in birds is capable of limiting the clutch of eggs laid. It is in some way dependent on the number of eggs in the nest; but how it acts is far from clear.

In December and January, 1931-32, an attempt was made to determine whether the light affected the Starlings through the head. Light-tight hoods were placed upon half the birds in a cage while added exposures to light were made. But all the birds in the cage died from the necessary handling of the birds to put on and take off the hoods, and nothing came of it. From similar experiments with ferrets, however, using hoods with and without eyeholes, it was evident that for them the eyes were the receptors for sexual photic stimulation (Bissonnette, 1936d). Benoit (1934, *et seq.*) has shown that for the duck the eyes are the normal receptors; with eyes removed, the exposed ends of the optic nerves may act as receptors; even the hypophysis itself may be stimulated directly by light to induce sexual activation; but only when thyroids and hypophysis are present. He also found that the red end of the spectrum was effective but not the blue-green regions. Ivanov (1934), however, concludes that in sparrows even denuded skin may act as receptor for this reaction. Martin, Buchner, and Inkso (1933) found that if combs were removed from cockerels their wattles and testes enlarged considerably. So the reception of sexually stimulating light was increased.

The first account of use of night lights to induce autumn and winter laying with poultry dates back to a Spanish book of 1802. Waldorf in 1905 was first to use it in this country (Lippincott and Card, 1934). The response is evident in ten to twelve days. But fowl may be bred to high winter production without night lights and the poorer layers are the most improved by increased light (Whetham, 1933; Kennard and Chamberlin, 1931).

Warren and Scott (1935, 1936) and Scott and Warren (1935) have shown that, among the factors influencing ovulation rate in the hen, light is an important one.

Miyazaki (1934) showed that the mejiro, a green bird of Japan, can be brought into sexual activity and caused to sing its mating song at least three times a year instead of once by night-lighting or "yogai" as it is called. Reduction of daily periods of light leads to molting.

Petty (Brill, 1934), in Oklahoma, induced the Bob-white quail to lay from January 1 in one year and December 3 in another by increased lighting and controlled temperature and humidity; and one hen laid 167 eggs before stopping. He also induced them to "group mate" with two cocks and seven hens, with fertility just as high as with pairs. Fertility and hatchability were good and growth better than normal. Bissonnette and Csech (1936a, 1936c) independently induced Bob-white to lay outdoors from March 22 instead of May 19, in Hartford, Connecticut, with fair fertility and some hatch, without control of temperature or humidity.

Martin (1935), with continuous light from 5:00 P. M. to 6:00 A. M. and feeding for egg-production, from December 5, induced laying beginning January 1. Cold weather did not hamper egg-production. No eggs were fertile before three weeks of laying but after that fertility was high, especially after days began to be warmer in late winter.

Clark, Leonard, and Bump (1936, 1937) found that pheasants, quail, and ruffed grouse all responded to increased illumination in winter by enlargement and activation of the gonads, but failed to continue long enough to secure laying. Bissonnette and Csech (1936a, 1936b, 1937) induced Ring-necked Pheasants to lay fertile eggs beginning on January 15 by gradually increasing their periods of daily illumination from December 16, and induced three hens to lay an average of 105+ eggs each before June 29. The hens, but not the cock, were apparently exhausted by this activity and after ceasing to lay they all died soon after return to the normal daylight conditions. In another experiment five hens and a cock hatched on May 7 were subjected to increasing night-lighting from 151 days of age, October 5. One hen began to lay at 185 days of age on November 8. Ten of the eleven eggs she laid were set and gave 50 per cent fertility and 30 per cent hatch on Christmas day. In nature these birds would not have laid till controls did at April 4 and 5, or about 332 days of age. All these birds were in pens smaller in dimensions than those of controls. So their freedom to exercise was curtailed though it was doubtless prolonged each day. In some later experiments in which similar periods of lighting were given but two pens were subjected to greater disturbance from the public and from observation generally than another pen placed between them, the least disturbed or least exercised pen was the one to lay most consistently and prolifically. Greater exercise and disturbance did not lead to earlier or greater sexual activity (unpublished data).

Sparrows, recently tested by Keck (1932, 1934), Ivanov (1934), Kirschbaum and Ringcon (1936) and Riley (1936), show sexual photoperiodicity. They also show evidence of refractoriness to stimulation in early autumn just after the breeding season, which is not shown by young birds of the season's broods. Witschi and Riley take this to minimize the effect of light as a factor in modifying sexual cycles. But it would seem better to regard it as a reaction against maximum activity which causes lowered susceptibility to photic stimulation. It also indicates that young sparrows in their first year would come into breeding in autumn but for the retarding influence of shortening days. Ivanov's finding that denuded skin as well as eyes may act as receptor in sparrows has not been confirmed by others. Ringoen and Kirschbaum (1937) found that covering the eyes of sparrows prevents even seven hours of added light from inducing spermatogenesis in November when controls were completely activated.

Recent work on mammals and birds indicate that sexually photoperiodic animals, as well as others, have inherent cycles of the anterior pituitary and of gonads, etc., dependent on pituitary activity, which, in the absence of effective environmental factors to modify and synchronize them with the seasons for optimum reproductive success, control the reproductive and other rhythmic activity. Phases of these cycles may be accelerated, initiated in periods of normal quiescence, retarded, or delayed by one or even many environmental variables, of which changes in daily duration, intensity, and wave-length of light and changes in types and constituents of food are two.

The peculiar sexual behavior of migratory birds will be discussed below along with other phases of migration phenomena.

MIGRATION

This form of photoperiodicity has been ably reviewed by Rowan (1926, 1931), Wetmore (1932), Kendeigh (1934), and Thomson (1936) and some additional facts in relation to transequatorial migrants have been brought out by Marshall (1932, 1936, 1937) particularly in his Croonian Lecture and the supplement which followed it. These relate to the special types of sexual photoperiodicity of birds whose migration across the equator and failure to breed in their winter range have been such stumbling blocks to those formulating theories as to its cause and its general relation to more common forms of migration. It is difficult to discuss migration except in correlation with sexual photoperiodicity, because Rowan's work has shown that the two phenomena are closely correlated, in some birds at least. One might well add that tendency to form summer and autumn flocks is also related to these phenomena. Therefore it is impossible to avoid some overlapping of the following upon the preceding topic.

Riddle, Smith, and Benedict (1932) suggested that the thyroids of migratory birds fail to respond to onset of cold weather by increasing activity while those of non-migratory ones do. Migratory birds have higher metabolic rates than do non-migrants. Kendeigh (1934) believes that spring migrations correspond secondarily with the prevalent temperature of the season; when spring temperatures average higher than usual migration is earlier, and later when temperatures average lower. This is difficult to separate from brighter days due to less overcast skies.

Sharpey-Schafer (1907), as quoted above, points out the need for a regularly recurring environmental stimulus to condition migration such as regular increase and decrease of length of day in spring and autumn. But he felt sure sex-gland fluctuations are not its fundamental internal cause, because in spring migrants these glands are but little larger than in autumn. With this Eifrig (1924) agreed.

Rowan (1925-37), however, in a series of very ingenius experiments with juncos and crows, was led to the conclusion that, for these species, the change in length of day in autumn causes the regression of the gonads which brings on the southward migration or perhaps more properly the restlessness which leads to migration. He concluded that increase in activity of these glands in spring induced by increasing daily exposure to light causes the spring restlessness leading to migration northward (Wagner, 1930). His experiments with crows are suggestive rather than conclusive. at least in regard to northward migration. His conclusion that the birds migrate southward when their sex-glands are either regressing or just regressed and northward when they are becoming larger and more active is supported by Wagner's (1930) finding that caged migrants show pronounced activity at night only at the spring and autumn periods of migration. Rowan's results indicate that temperature is not a major factor in the induction of sexual activity or its suppression. to which he attributes migrations, though Kendeigh (1934) appears still to consider temperature changes a major cause of migrations. Rowan is supported on the temperature question by Bissonnette (1930-1933) and Bissonnette and Wadlund (1931-1933) with Starlings, Cole (1933) with Mourning Doves, Miyazaki (1934) with Mejiros, Petty (Brill, 1934) with Bob-whites, Martin (1935) with pheasants. Clark, Leonard, and Bump (1936, 1937) with pheasants. Bob-white. and grouse. Bissonnette and

Csech (1936-7) with pheasants and Bob-white, Benoit (1934-6) with ducks, and Scott and Payne (1937) with turkeys.

Moreau (1931) and Bissonnette (1932c, 1933, 1936c) have suggested that change in type or scarcity of food may act as a limiting factor though not as an activator, when it becomes inadequate to support reproductive activity. Witschi (1935) denies this, without reservation of any kind, on the basis of the fact that his African weaver birds retained their breeding cycles on a constant food ration for three years in Iowa City. But they were evidently on an adequate diet all that time. That they did not change their cycles does not prove that even their cycles can not be modified by changes in feeding régimes just as Bissonnette's Starlings on inadequate diets were prevented from responding completely to sexual activation by very stimulating exposures to even red light, to which, on adequate and varied diets, they are most responsive. Witschi's birds responded sexually to the inherent cycle of the anterior pituitary without modification by changes in light cycles. Scott and Payne (1937) had already found that the guinea fowl, a native of the tropics, is not sexually responsive to added lighting out of its normal breeding season (Bissonnette, 1936c). Blinded ferrets also show failure to respond to increasing daily exposures to light (Bissonnette, 1937) but show an inherent cycle of sexual activity and quiescence, which, however, cease to be correlated normally with the seasons, as they are with intact eyes. This mammal has a seasonal sexual cycle, like the Starling, conditioned and modified by seasonal changes in length of day. This conditioning is removed by cutting the optic nerves and the animals behave like Witschi's weaver birds do naturally. It is evident, therefore, that in some birds and mammals the inherent cycle of the sexual apparatus is more fixed than in others and less susceptible to environmental interference or less responsive to different environmental factors of which change in length of day and change in food are merely two (Bissonnette, 1935, 1936c). As Bissonnette has pointed out, these cycles are conditioned by various factors in addition to the internal rhythm, depending on the evolutionary and environmental history of the animals concerned.

Rowan (1929, 1936) concludes from his experiments that the migration in autumn is due to shortening days acting not as reduced photic stimulation but as reduced periods of exercise or bodily activity inducing shrinking and decreasing activity of the sex-glands; the spring one to increasing daily periods of exercise, not increasing photic stimulation, inducing enlargement and activation of the sex-glands. With this phase of his theory of migration and sexual photoperiodicity

Bissonnette and his co-workers and Benoit (1934-6) and some others are not in agreement. Nor is it certain that the sex-glands are necessary to the migration cycle. That the anterior pituitary is a necessary part of the mechanism is more probable in the light of recent research and of Rowan's experiments on crows. The probability of an inherent cycle of high and low sexual activity resulting from a similar cycle of activity of the anterior pituitary can not be overlooked in view of the regression of sexual activity in Starlings before June 15 in nature (Bissonnette, 1931, *et seq.*) while days increase in length till June 21 and in luminous intensity till later in the summer. Similar regression also occurs in Starlings, ferrets, fowl, ducks, raccoons, and other birds and mammals under experimental lighting schedules, and also under continued injections of gonadotropic hormones from the anterior pituitary and pregnancy urine (Bissonnette, 1936c).

For birds that do not migrate into the tropics or across the equator, Rowan's hypothesis with the above reservations seems to fit the cases better than any combination of factors including temperature and food yet suggested. Considerable evidence is accumulating, however, that sexual cycles, in birds, mammals, and some other animals, and, probably, migration cycles in birds depend on inherent rhythms of the anterior pituitary more or less fixed in the absence of, or without responsiveness to, external, usually stimulating, factors like light cycles (Bissonnette, 1930-37; Hill and Parkes, 1933, 1934; and others). In many animals, in nature with normal exteroreceptors, these cycles are synchronized with the seasons by response to external factors, of which light cycles may be only one, depending on species, length of incubation or gestation period, and/or the degree and rate of change in the effective intensity of the external factor (Bissonnette, 1935, 1936c; Witschi, 1935; and others). For example, while increasing light activates or accelerates sexual activity in Starlings and ferrets, the sex-glands of Starlings on normal light cycles go into regression before the maximum length or brightness of day in June, and both Starlings and ferrets go over into sexual regression after a time even in spite of experimentally lengthening days and can not be maintained in continuous maximum activity by increasing duration and intensity of light. They become refractory to this type of stimulation and for a time incapable or much less capable of a second stimulation or require much greater degree of stimulus than before the refractory condition sets in or longer time to be activated again. Riley (1936) has shown that this is also true for sparrows. Their susceptibility to stimulation then increases again and, in the absence of increasing light as a stimulator, the pituitary may again become active, though at a slower rate and later in time than with light or other stimulating factor to accelerate its action (Bissonnette, 1937). Bissonnette's experiments with Starlings and Benoit's (1934-1936c) with ducks indicate that it is light *qua light* and not increased waking periods or exercise that is the major factor directly concerned. Both find that not only is increasing length of day a factor but also increased intensity and larger amounts of the longer-waved rays near the red end of the spectrum. The shorter-waved blue and green are ineffective to stimulate Starlings or ducks; but, with ferrets, all the visible and a little of the very near ultra-violet are apparently equally effective to induce sexual activity (Marshall and Bowden, 1934-1936). This points to species differences in this matter. As pointed out above, Scott and Payne (1937) have shown that for turkeys the light must be of additional duration and not merely added during the day as increased intensity of illumination, possibly because given in that way it is not enough of a relative increase to induce increased response. Marshall and Bowden have shown that if the intensity times the time of additional lighting is kept constant the resulting acceleration of sexual activity in the ferret is approximately constant. If the additional duration is zero, perhaps that would account for Scott's results since additional duration is reduced to zero and the product is therefore also zero.

Kendeigh (1934) has shown that direct endocrinal stimulus is important in migration and he believes the hormones from the gonads, varying as part of the reproductive cycle are most important. Keck (1932, 1934) and Witschi (1935, 1936) have shown that sexual changes in birds are dependent upon pituitary hormones. Benoit (1937) finds that the thyroid is involved as well as the pituitary. Castration lowers metabolic rate as does decrease of thyroid activity (Mitchell, Card, and Haines, 1927; Aude, 1927). Wachs (1926) believes that the physiological rhythms concerned are independent of or related only in time to environmental changes. Length of day or change of intensity of light can have little causal relation to the return of trans-equatorial migrants. Species differ in regularity and types of migration. We agree with Kendeigh that climate includes factors of major importance in controlling migration, distribution, abundance, and behavior responses in many birds. We would add that of these factors changes in duration, intensity, and even wave-length of light with the seasons and the development of refractoriness to the activating factors are of paramount importance, for many species.

Thomson (1936) points out the "inter-migrations" which are superimposed upon the primary or great migrations of many birds. These may even be reverse migrations. They occur in response to adverse weather conditions among weak migrants and do not occur among strong migrants which will succumb to bad weather without retreat. "Abmigration" in ducks is a northward migration in spring by birds that have remained over winter in their original breeding areas. These, with exaggerated migrations by some birds, may lead to invasion of new territory in some seasons. They may also be mere food expeditions and not migrations in response to the normal migration-inducing stimulus. They may depend upon fluctuations in food supply like the invasions of New England by snowy owls about every four years which correspond to the years of maximum population of arctic foxes. These movements are not usually directly north and south. Migrations from more to less arid regions in the tropics, even across the equator, may be of this sort. In Africa, some species are found both north and south of the equator and breed in opposite seasons in the two localities. Some breed in the north of their range and some nearly related species in the south part of their range. One species crosses the equator and breeds in the south and so can feed on winged termites almost throughout the year. This is related to changes in humidity.

The order in which the two sexes and ages reach the summer territories varies with different species. In some, males precede, mixed groups next, and females alone last. In some the first are all young, and old males are last; in some the young come first, then mixed old and young (Starling) ; in others old birds only, then mixed old and young, and only old birds again last. Rowan showed that adults precede young birds in autumn among juncos, females first followed by flocks of males; the reverse is true in spring. Among golden plover, young birds take a different route and a different time from the old birds. These cases show differences in reaction of physiologically different members of the same species and also sex differences.

Van Oordt (1928, 1931) showed that birds failing to complete spring migration usually have winter or intermediate plumage and inactive sex-glands, which may be due to vagaries of the anterior pituitary. Gotz (1929) found that, if there is an autumn molt, migration follows it immediately; that delayed breeding is followed by delayed molt and migration; that passerine birds with two molts per year are usually migrants. Others see less correlation of molt and migration, since individuals in some species differ from others in relation of molt to migration. Some spring migrants are even losing body feathers while migrating. Both molt and migration are probably related to the rhythm of the pituitary sometimes in different ways, even depending on the previous experiences of the individual bird. Segregation of species is often shown in large migrating mixed flocks. Few sing on the northward spring flight; none in the autumn flight. Particular communities of some species take different routes habitually and this may lead to extermination of some groups with survival of others. Different routes are often taken by the same birds in spring and autumn. The origins of migration and of these specific and individual differences is beyond the scope of this paper.

Native born Starlings in England do not migrate (Wynne-Edwards, 1929); neither did these birds for some time after introduction into America. But of late they are beginning to do so. Migration can not be a learned habit because in some species the young precede their parents and in some they follow. Thomson (1936) believes that two factors are acting as stimuli to migration; physiological cyclic changes in the bird and seasonal extrinsic factors in their environment. He points out that reversed migration in Rowan's Crows occurred in only a few birds but that they followed the direction usually taken by Crows in their normal migrations. Castration did not inhibit these migrations. He thinks Rowan may be overstating it when he concludes that the southward migration is independent of the gonads, though it is probably so for young birds of the year. He fails to consider the complete results of Bissonnette's work in its bearing on Rowan's conclusions and apparently knows nothing of Benoit's studies on the duck, cited above, and their support of Bissonnette's findings.

Thomson points out, as we did above, that both Rowan's and Kendeigh's theories of migration require modifications to suit transequatorial and other types of migration mentioned above. He agrees with Moreau (1931) that periodicity differs with different species of migrant; that daylight changes apply only to migrations of birds from temperate regions and only in autumn to transequatorial migrants from temperate zones whose spring migration is governed by an internal rhythm which over-rides external factors; that in birds confined to the tropics some other factor or factors must operate. He says the "periodicity is essentially the same in all cases, but it may become linked with different factors in the environment according to circumstances. The inter-related reproductive and migration cycles may both be expressions of a periodicity reflecting the influence of all the external conditions governing the bird's life; the phases of these cycles may be induced by environmental stimuli of different kinds, or may occur to some extent without extrinsic stimulus by virtue of an inherent rhythm. In some such way the hypothesis of a primary stimulus from the reproductive system may be given general application to various categories of migratory birds". According to our hypothesis, which will be stated below, we need only change "reproductive system" to endocrine system of the anterior pituitary and related glands.

Chapman (1928) points out that the last migrants to arrive are in general the first to leave and that corresponding dates of arrival and departure tend to be approximately equidistant on each side of the summer solstice. He feels that the state of the reproductive organs prompts birds to migrate to nesting sites.

Stimmelmayr (1932) suggested that a particular declination angle of the sun in both autumn and spring is the critical factor in each case acting through atmospheric electricity, just as he ascribes orientation for the homing reaction to electric currents not as yet demonstrated. But Besserer and Drost (1935) have shown that, with these possible electric factors excluded by insulation of the cages, the birds still show "migration restlessness".

Thomson (1936) thinks that, for most cases of migration, weather is capable of acting only within narrow limits on birds already stimulated by the primary factor to a state of unrest. For those with "weather movements", however, it may act as more than a secondary stimulus. The autumn departure date is modified by falling temperature and high barometric pressure in conjunction with individual physiological states (Nice, 1933). If approximate date of migration depends on seasonal rhythm of the bird and its environment, and exact day on immediate weather conditions, the precise moment of flight often depends on intensity of light, even to a particular degree of twilight for nocturnal migrants (Drost, 1930, 1931).

As to path of flight on migrations, Stresemann (1935) suggests that the angles of inclination and declination of the earth's terrestrial magnetism at different places acting on statoliths in the birds' ears may act as a stimulus to guide them on flights till the right ones are reached. But, since members even of the same brood may migrate in different paths, there would seem to be no general rule operative in all cases. This may or may not be related to light. We have not enough data to decide (Thomson, 1936).

If one may be at least condoned for attempting to put forward as a working hypothesis a suggestion as to the interaction of intrinsic and extrinsic factors in bringing about migratory flights and failure to breed in the winter range, the following may be of some interest and stimulation to further study of sexual and migratory photoperiodicity.

Recent research on the physiology of the hormones of the anterior pituitary, gonads, and thyroids indicate that there is, in many animals at least, an inherent rhythm of activity of the pituitary of varying duration of cycle and of phases of that cycle. The gonads, accessory sexual apparatus, and behavior are subject to control by the pituitary and thyroid as shown above. This rhythm is in some animals capable of stimulation, inhibition, or retardation by extrinsic factors of which changes in daily periods of light and in food are two. If so, or if not, the sex-glands and pituitary reach a maximum phase of activity but can not be maintained beyond a time which varies with the species and the rate at which they have been caused to come to this maximum. The whole complex of endocrine action on which the sexual cycles depend goes over into regression of varying rate and degree and a refractoriness of varying duration results. These are the facts.

The sexual and migration cycles are corelated with those of plumage and the pituitary-thyroid complex. If the progress of regression of pituitary and gonads during the refractory phase, which develops with or without extrinsic inhibition, or even in spite of stimulation by increasing days or other lighting changes, is slow and of considerable duration and if flocking and southward migrations of many birds are dependent on it, the southward flights may take the birds to or beyond the equator. Rate of flight may also help to determine the distance flown southward. If in young birds of the year shortening days induce an autumn regression of the pituitary when activation would otherwise occur, their first southward flight will be accounted for. If the refractory period of this endocrine system is prolonged after southward flight stops and before the recovery phase of the cycle begins, also more or less spontaneously, or the birds become responsive to longer days, failure to breed in the southern or winter range results. Detention in that range, however, should be followed by a breeding cycle there. That this does occur with European storks in captivity in Lima, Peru, has been pointed out by Murphy (1925, 1936) and Marshall (1937).

On recovery of the pituitary, begun even with days not increasing, or when not completely inhibited by a steep enough falling gradient of day-length or other factor to which the birds respond, the birds would be stimulated by pituitary activity to the reverse reaction and fly northward or toward their summer range before or while their sex-glands begin progressive changes which culminate, or reach such a point as to induce migration to stop, and mating, nesting and incubation to occur, at a time and place depending on the species and perhaps on their original birthplace and region of early acclimation (Cole, 1933). These last functions are conditioned by hormones from the anterior pituitary (Riddle and his co-workers).

This return to activity of the pituitary and sex-glands may occur in some animals even in spite of great reduction of effective day-length as indicated by experiments on ferrets, mammals whose sexual cycles are partly controllable by changes in daily lighting just as are those of juncos, crows, starlings, canaries, doves, mejiros, ducks, etc. (Hill and Parkes, 1933, 1934; Bissonnette, 1936c, 1937; Benoit, 1934-6).

Prolonged refractory periods following maximal activity with or without environmental stimulation by light or other factors, would supply the necessary delay to prevent even trans-equatorial migrants from breeding in their southern range. Recovery of the activity phases of the pituitary cycle, even without environmental stimulation at first, will account for the start northward and the reactivation of the sexual apparatus, in various degrees of correlation with each other, depending on the evolutionary history of the species.

This would give a single theory to account for the behavior of all true migrants, whether controlled by seasonal changes in illumination or not. But much testing, both in general and in detail must be done before this theory can be more than a working hypothesis. That it is reasonably easy to test, both experimentally and by observation of birds and their movements in nature, is beyond question.

That the primary agent to modify the cycle is change of periods of exercise is improbable in view of Bissonnette's and Benoit's studies. Also, the long-continued flight southward, coming in some birds at night after feeding by day, would induce reactivation of the gonads if increased exercise were the major factor inducing northward migration and sexual activity, if the refractory period were not too pronounced to be overborne by it. In fact Rowan's castrated Crows migrated southward in the autumn condition (Rowan, 1932). This would suggest that the cause is more fundamental than the reactions of the gonads. One thinks of the anterior pituitary as the more fundamental agent.

Cole (1933) suggested that different geographical groups of some species may vary in their response to light;hence their distribution; though light is not the only factor operating (Bissonnette, 1932, '33, '35, '36; Davis, 1933; Lock, 1933; Linsdale, 1933; Witschi, 1935). Variations in their refractory periods and in the time at which they reach mating and nesting phases of recovery would account for their place of taking up these activities and for their summer distribution. This may be related to their birthplaces and early conditioning during their first summer. Bissonnette (1935, 1936c) suggested this probable control of migration by the anterior pituitary, and Allard (1928) suggested that length of day is the probable environmental factor most concerned in setting off migration urge, but that it could apply only to birds subject to lengthening days in spring in their southern range and also during their northward flight.

It is likely that different species are conditioned by different factors in their environment, some already known, others not yet determined; and the same species may be responsive to more than one factor. Enough importance has not hitherto been given to the occurrence of the refractory state or phase after varying periods of maximum activity of the endocrine systems. These develop in spite of increasing intensity and duration of the normal extrinsic stimulus. The degree and kind of response differs in different species. The inherent rhythms are perhaps more dependent on this regularly recurring refractoriness with temporary regression than upon the occurrence of recurring stimulation. Recovery may be, and probably is, spontaneous in the absence of conditioning by external factors or when animals are not inhibited by decreasing amounts of stimulation. The frequently repeated cycles of polyoestrous animals including birds may well be determined by the quicker arrival at the refractory phase followed by quick recovery without great susceptibility to stimulation or inhibition by external factors or changes in them. This may be the determining factor in birds that have two or more broods per year in contrast to those that have but one. It may also in different degree be responsible for the different times at which different species and even different groups of the same species begin their flights in migration. Age and sex differences may furnish the physiological differences in condition which cause one bird to react at one time, another at another. It would also account for the different times at which birds arrive in the spring.

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THE MOCKINGBIRD IN WESTERN SOUTH DAKOTA

BY CLAUDE A. BARR

The arrival of Mockingbirds at our grove in May, 1936, brought to us the pleasant expectancy of a number of days of unusual entertainment, and the recollection of visitations of other years, but no more than a promise of the eventful season of observation and enjoyment that was to be ours.

In our twenty-six summers on the plains, Mockingbirds (it is the western form, *Mimus polyglottos leucopterus*, with the larger white wing patches, which comes to this southwest corner of South Dakota) had been rare. The first was noted perhaps twenty years ago, unmistakably, for we had known the Mockingbirds of Arkansas and Illinois. He stopped for a morning's rest and inspection of the relatively new homesteads and young trees. The tally of those that had been seen prior to 1936 was no more than seven, including two pairs in different seasons. One pair had remained for thirteen days.

On the morning of May 2 bold and ringing notes were heard, and the new visitor was eagerly sought out, for to be able to see and to